GLOBAL CHANGE AND CORAL REEF ECOSYSTEMS

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INTRODUCTION

This paper reviews known or probable responses of coral reef ecosystems to "global change." Our focus is on the coral reef ecosystem, and on its defining organism, the symbiotic stony (scleractinian or milleporid) coral. One of the unique features of coral reefs is that the communities are commonly supported by biogenic geologic structures of their own creation. This creation of substratum by a taxonomically circumscribed group of organisms provides a dimension of interaction between community and environment not found in most other ecosystems. Other groups of organisms are also important to the structure and function of coral reefs; however, in most cases either functional roles are fulfilled by so many different taxa that it is impossible to generalize about responses to environmental variables, or there are very few data on which to base assessments of effects on them.

Individual organisms and ecosystems respond to their local environment without regard for the ultimate cause of environmental conditions. It is often not possible in practice to distinguish between the effects of climate change, of natural environmental variability, or of non-climatic anthropogenic alteration; effects may be interactive, or a single stress may have multiple sources. We use the term "global" in a broad sense, to include global climate change (the so-called "greenhouse effect"), non-climatic but global environmental changes such as the degradation of stratospheric ozone, and changes that can be called global in the sense that they are widespread, sustained, and likely to increase in distribution and intensity—the many effects of population growth and economic development. We emphasize that "global" does not mean

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uniform, monotonic, or ubiquitous. We focus primarily on the nature and directions of present or reliably anticipated environmental change—warming and sea level rise rather than the onset of an ice age, increases rather than decreases in ultraviolet light, and so forth. Finally we focus on changes to be expected within the next century, rather than on longer-term or even less predictable effects.

This review shares with most reef-oriented research an intrinsic bias toward negative effects and stresses. If one starts with a "healthy" coral reef, there are many ways things can go wrong, but only a limited spectrum of "improvements" can be envisioned. Future reef communities may propagate to and thrive at sites not presently classified as coral reefs, but direct observations or specific predictions of such occurrences are—and seem likely to remain—restricted.

Global Change Scenarios

A brief summary of the status of global climate change predictions provides a context for subsequent discussions. We rely primarily on the work of the Intergovernmental Panel on Climate Change (78), and on MacCracken et al (106), who combine discussions of model-based predictions and paleoclimate records. This is a rapidly developing field. Although the detailed predictions derived from general circulation models are uncertain and subject to revision, there can be little doubt in a qualitative sense that the increased and still-increasing concentrations of radiatively active gases in the atmosphere will result in significant climate change of some sort.

Under the IPCC "Business as Usual" scenario (i.e. no substantial changes in present trends in greenhouse gas emissions), global mean temperatures are predicted to increase during the next century by about 0.3°C per decade (range: 0.2–0.5°). The net increase will amount to about 1° by 2030 and 3° by 2100. Land surfaces will warm faster than oceans, and high northern latitudes will warm more and faster than the global mean, especially in winter.

Present confidence in regional climate change predictions is low. In the oceanic tropics, the area of most interest to this review, the predictive ability of the general circulation models is highly questionable; both between-model agreement and calibration against present conditions are poor. Some models predict tropical sea-surface temperature increases of 1–3°C, but there is widespread debate about possible feedback mechanisms that might either stabilize values in the vicinity of 30–31°C (73, 123), or produce positive temperature feedbacks over the warmest part of the ocean (54). Although paleoclimatic conditions are not generally considered reliable predictors of future climate patterns, it may be relevant that during the Eemian warm period (125,000 BP) most northern hemisphere land areas were significantly warmer than at present, but tropical regions were not detectably warmer (106, 127).

Also under the IPCC Business-as-Usual Scenario, global sea level rise is predicted to average about 6 cm/decade over the next century (range: 3–10 cm/decade); this value compares with recently observed values of 1–2 cm/decade, and with maximum sustained rates of sea level rise during the Holocene transgression in excess of 20 cm/decade (7, 51).

Changes in the frequency and intensity of extreme events are probably more ecologically significant than moderate changes in the mean values of environmental factors. In addition to a probable increase in high-temperature events, two possible changes relevant to local coral reef environments are worthy of note (110). One is a shift in precipitation patterns so that more of the total precipitation falls during heavy storms; the other is a possible change in the frequency, magnitude, or geographic distribution of major tropical storms.

ECOSYSTEM ROLES AND RESPONSES

Ecosystems and their responses to environmental change may play various roles in a climate and global change context. Ecological control of reservoir size or rates of flux for climate-influencing materials such as CO_2 is a potentially important factor. In relation to human society, ecosystem sensitivity—or vulnerability—is an important issue; ecosystem collapse in response to environmental change may result in loss of resources; degradation could, in principle, serve as an early warning of increasing stress. From a scientific standpoint, large-scale environmental changes represent a natural experiment that may permit investigation and understanding of ecosystem structure and function not possible on a laboratory scale or in a stable environment. In this section we discuss these three issues before turning to a more detailed inventory of coral reef responses to individual environmental forcing functions.

Geochemical Reservoirs and Fluxes

Some systems, such as tropical rain forests, represent substantial global reservoirs of carbon. Temporal changes in the mass of such systems may be significant in terms of the atmospheric CO_2 reservoir, and such changes can provide feedbacks that may enhance or retard climate change forcing by atmospheric CO_2 or other biogenic gases. The $CaCO_3$ of coral reefs and other oceanic ecosystems represents another large carbon reservoir. Calcification represents the largest net carbon flux term associated with coral reefs (29, 94, 155). We therefore use reef calcification in order to assess reef significance to the global carbon cycle.

There is a widespread conception that coral reefs and other aquatic ecosystems dominated by calcifying organisms are sinks for atmospheric CO_2

(22, 95, 148). On time scales of human interest, $CaCO_3$ precipitation by aquatic ecosystems approximately in equilibrium with atmospheric gases is actually a source of CO_2 release to the atmosphere, rather than being an atmospheric CO_2 sink (155). This counter-intuitive result arises because $CaCO_3$ precipitation lowers pH and converts bicarbonate to CO_2 gas. If the water comes to gaseous equilibrium with the atmosphere, then CO_2 gas must escape from the water to the atmosphere. For coral reefs, the effect of calcification on the overlying atmospheric composition is small (59, 94, 155) and to some extent offset by CO_2 uptake from the atmosphere as a result of net organic carbon production (139, 144, 155). Reefs at steady state are a "greenhouse CO_2 source" of about 4×1012 mol/yr, equivalent to about 1% of the CO_2 released to the atmosphere by anthropogenic activities. Although diminution of marine net calcification could increase the uptake of atmospheric CO_2 by the oceans, coral reef contributions to the atmospheric CO_2 flux are well below the uncertainty levels of the major sources and sinks.

Ecosystem Sensitivity

SENSITIVE VERSUS ROBUST ECOSYSTEMS   Widespread observations of apparent coral reef degradation (32, 158) have led to an ongoing debate as to whether reefs are "fragile" or "robust" ecosystems (34, 43, 44, 66).

The argument for robustness stems from geological evidence and from certain contemporary theories and observations of reef community development. On evolutionary and geologic time scales, it is argued that physical conditions are primarily responsible for mass extinction events (124), and that the climatic factor most responsible for mass extinction is refrigeration (145). In spite of common perceptions that reef biota are more vulnerable to major extinction events than are other marine organisms (83), this view has been contested (124, 131).

Maximum rates of sea-level rise during the Holocene exceeded 20 cm/decade during two separate periods lasting for roughly 1000 years each (7, 51). The difference in global mean temperature between the last glacial maximum and the present interglacial has been estimated at about 4°C (106), while the comparable difference of maximum temperatures in tropical marine environments ranged from <2° to 4° (127).

Similar fluctuations have occurred repeatedly throughout the Pleistocene. The persistence of coral reef communities as an ecosystem type (although not as temporally continuous individual communities) across repeated changes of these magnitudes suggests that reef ecosystems as a global phenomenon are not likely to be threatened by the predicted greenhouse-effect. The Quaternary climate oscillations occurred, however, on time scales that are long compared to the lifetimes of reef organisms, while greenhouse-forced global temperature change is predicted to be at least an order of magnitude

faster—placing it on the same decadal time scale as coral lifetimes and community turnover.

Paulay (119) summarizes work indicating that while Plio-Pleistocene total extinctions of both corals and mollusks in the Caribbean were in excess of 30%, western Indo-Pacific faunas experienced extinctions of only 10–15% of corals (118, 152) and 20% of mollusks (rates described as "background levels") . Paulay's studies of the responses of Pacific island marine biota to Late Pleistocene sea level changes indicate variable patterns of local extirpation and recolonization, but with little large-scale permanent loss of diversity. Potts (122) has addressed the related issue of coral speciation and argues that it may be controlled by the relationship between longevities or generation times and the time-scale of habitat destruction.

A number of descriptive and theoretical approaches to coral reef ecosystems have indicated that reef communities are adapted to intermittent disturbances (27, 42, 44, 65, 66, 146). Indeed, disturbance may actually be necessary to the maintenance of a widely distributed healthy and adaptive ecosystem, analogous to the function of forest and grass fires in some terrestrial ecosystems.

In our opinion, the "robust vs fragile" debate is primarily the result of failure to define terms and conditions, particularly with reference to scale. The coral reef ecosystem, on a global scale and as a class of communities, is clearly robust with respect to natural climate change and variability over periods of millions of years. This robustness, coupled with wide geographic distribution and the possibility of range extensions to currently unsuitable environments as a result of global warming and sea level rise, suggests that the reef ecosystem is unlikely to be extirpated on a global basis by global climate changes currently predicted.

Reef fragility, however, is real and is a legitimate concern on time and space scales significant for human society. The robustness of reefs as a class of communities on a large-scale, long-term basis does not address specific concerns about the future of existing reefs as they respond to present-day stresses. Past natural stresses may not be adequate proxies for future accelerated climate change, which will occur on time scales much more comparable to the generation times of major reef organisms than was the case for past natural climate fluctuations. An even greater concern is the increasing extent of non-climatic anthropogenic stresses that reduce available refugia (83), impose stresses to which reef communities are not particularly well adapted (e.g. nutrient loading and sedimentation), and may interact with or exacerbate the more survivable climatic stresses.

ECOSYSTEMS AS "EARLY WARNING BIOINDICATORS   Sensitive ecosystems or organisms may be "early warning systems" of environmental or global climate

change. Such a role has been suggested for the "bleaching" of corals on coral reefs.

"Bleaching" has long been recognized as a coral response to various forms of environmental stress (17). This process may involve the loss of pigmented symbiotic algae (zooxanthellae) from the host coral, or of pigmentation from the retained algae (76, 86, 149); the physiological and environmental significance of the two modes of bleaching are not fully understood, and they are not readily distinguished by field observations. Corals without pigmented zooxanthellae appear white, or "bleached." Bleaching can be induced by a variety of stresses, including high or low temperature, salinity depression (and probably elevation), and excessive solar radiation or excessive shading. Bleached corals exhibit reduced production: respiration (P:R) ratios, reduction or cessation of calcification (121), and interruption of reproductive activity (149). If mortality does not result, apparent color recovery typically occurs within a few months, but long-term physiological recovery may be delayed for over a year (53, 149). Repeated bleaching on short time scales may result in increased cumulative mortality (130).

Extensive observations suggest that thermally induced bleaching and mortality, and subsequent community responses, have resulted from the unusually strong 1982–1983 El Niño (19, 56, 57, 60, 157). Other bleaching events, especially in the Caribbean have also been ascribed to high temperatures (19). Bleaching may be an early response of coral reef ecosystems to climatic warming (64). The evidence for both the temperature correlation and the climatic interpretation has been reviewed (32, 58, 59). Although episodes of regional or local high surface temperatures have surely been significant factors in major bleaching episodes, it is not possible to ascribe bleaching (or changes in its frequency of occurrence) solely to temperature. Given the definition of climate and our present understanding of climate change, short-term regional trends or variability in temperature or other directly measured environmental variables cannot be reliably ascribed to climate change (161). Thus far no rigorous explanation has been offered of how putative climate trends inferred from qualitative observations of uncalibrated biosensors can be more informative or reliable than direct quantitative measurements of the relevant variables.

Although not reliably useful specifically as a climate indicator, bleaching is a stress response and its occurrence is indicative of some form of environmental degradation or unsuitability (59). With adequate attention to diagnosis, mechanisms, and background levels of occurrence, it can be an important environmental bioindicator.

The Biogeophysical Experiment

Change in climate, or other large-scale environmental alterations, may be regarded as an experimental probe of ecosystem response, capable of yielding

information of both practical and theoretical importance. Buddemeier & Smith (21) and Hopley & Kinsey (77) have suggested possible reef responses to sea level rise that, either alone or in combination with other environmental changes, could provide tests of key ecological or geological hypotheses over the next century. On land, similar questions have been raised about how forest or agricultural ecosystems might respond to the effects of elevated CO_2 partial pressure, air temperature, and moisture. How does one perform or interpret an uncontrolled geophysical "experiment" on a time scale of decades?

A number of symptoms or indicators of change in coral reef environments may be identified as possible results of such an "experiment":

1. Incidences of disease, parasitism, morbidity, and mortality (from any or all causes) are direct measures of both organism and ecosystem health.
2. Growth, particularly the rates or patterns of skeletal growth of long-lived sessile organisms such as corals, is a useful indicator for which there is a background of knowledge about normal rates and environmental correlates that can be used for hypothesis testing in the event of significant change.
3. Shifts in community dominance or population structure are important indicators; of particular importance are shifts from calcifying to non-calcifying organisms, as in the case of algal invasions of coral communities in response to increased nutrient loading in previously oligotrophic systems. Other examples include changes in populations of indicator organisms such as filter-feeders or echinoderms.
4. Community metabolism is a measure of large-scale function that can be used to document functional changes over time or to determine whether the metabolism of a given community falls within normal limits. The characteristics amenable to such treatment include organic production, P:R ratio, and net calcification. The rates of these processes on unperturbed reefs appear to be remarkably consistent (90). Departures from the norm are therefore readily recognized.
5. The reproductive behavior of existing community members (spawning, etc) and the recruitment of new members (e.g. larval settlement) are involved in maintaining community structure and function and may be observed directly as indicators of environmental suitability or organism health.

The experimental utility of the above observable characteristics suffers from the drawback that reef systems tend to exhibit high natural variability in time and space, and we lack adequate baseline data. If we are to predict or learn from the effects of climate change, the research community will need to make a transition to a more quantitative large-scale perspective.

An important and closely related factor is that reef structures and organisms in reef systems are potentially very good recorders of change. For example, reef structures in the geological record have been used as indicators of sea

level and of relatively warm seawater. On shorter time scales, coral skeletons, especially massive forms, have annual growth bands analogous to tree rings, with some situations of subannual banding (8, 20). The bands themselves record variations in growth rate—which are in part responses to environmental variables such as temperature and solar radiation (103, 104). Moreover, the chemical, structural, and isotopic characteristics of the coral skeletons can reflect a wide variety of environmental forcing, with the growth bands serving as chronometers. The skeletal characteristics clearly can provide high-precision, uniquely diagnostic retrospective records at sub-annual intervals for periods ranging up to several centuries. Examples include information on river flow (81), oceanic circulation and turnover (45, 46, 132), and local stress events (121). Effective exploitation of these records can establish the baseline data needed to determine variabilities in reef environments on climatic time scales. A promising new approach to retrospective studies is the combination of population genetics with organism life histories and reproduction strategies to yield inferences about population dynamics over time (97).

REEF RESPONSES TO ENVIRONMENTAL VARIABLES

The sensitivity of corals, reefs, and related environments to environmental change, and their potential utility as monitors or recorders of change, is addressed in this section summarizing present knowledge about possible responses to changes in environmental factors. The order in which the variables are addressed is based on the level of certainty of near-term global change based on climate change considerations. Eustatic sea level rise and CO_2 concentration increases are extremely likely and globally equilibrated, and temperature increases are extremely likely although with significant uncertainty about regional variability. Other factors are considered to have a high probability of change but are either manifestations of climate change that are not predictable on a regional or local basis (light, physical oceanography, salinity) or are likely to result primarily from nonclimatic anthropogenic impacts (nutrients, sedimentation, resource utilization).

Sea Level

The predicted eustatic sea level rise (about 6 cm/decade) will be reflected in local relative sea level changes along with the influences of tectonism, atmospheric pressure, ocean current changes, and so forth. Coral reef responses to sea level rise need to be considered on two different scales. The potential exists for reefs to "drown" (i.e., be covered with such a depth of water that they are below the photic zone or otherwise cannot calcify sufficiently to catch up with sea level), but this requires a protracted imbalance between reef accretion rates and sea level rise. Depending on water clarity and other environmental conditions, the depth range of maximum reef

calcification may extend from several meters to more than 20 m. This depth range represents a safety factor; transient sea level rise may inundate oceanic reefs to a depth of meters or even tens of meters without terminating reef growth if sea level rise subsequently returns to a rate less than reef vertical accretion rates.

Reef vertical accretion rates calculated from community calcification rates, growth rates of calcifying organisms in reef communities, and radiometric dating of cores through reefs range from less than 1 mm/yr to a maximum slightly in excess of 10 mm/yr (21, 35, 36, 77, 92, 138). A rate of 10 mm/yr is commonly taken as the consensus value for maximum sustained reef vertical accretion rates (21, 36). The present best prediction for eustatic sea level rise over the next century is 6 mm/yr on average (156); this is well within the range of reef accretion rates, and even with no net accretion would submerge reefs by less than a meter by the year 2100.

On the shorter time scale of years to decades, sea level is a changing environmental variable that may interact with other changes and be reflected in organism and community response. Because sea level has been within 1–2 m of its present elevation for several thousand years, many present-day reefs have grown to an elevation where further upward growth is constrained by sea level. Sea level rise can be expected to remove this constraint and result in increases in successful recruitment and coral longevity on intertidal and shallow subtidal reef flats (77), with a consequent increase in reef flat calcification (94). If rising sea level creates more benign conditions on shallow reefs, diversity and community structure may change as species other than the extremely hardy are able to survive. Increases in coral community diversity and productivity can also be expected in enclosed lagoons where salinity extremes, nutrient depletion, or other aspects of restricted circulation have restricted reef development (119, 140, 141, 143), since the probable effect of rising sea level on circulation will be to maintain reef/lagoon water composition closer to that of the local oceanic water. On the other hand, if deepening water subjects currently sheltered communities to more physical (wave) stress, calcification and sediment accumulation may not increase (21).

Other possible effects associated with sea level rise may include shifts in zonation and community structure associated with the relationship between wave energy regimes and sea level in a given locale (31). (These issues are discussed in the Currents, Waves, and Storms section below.) Second-order interactions may also be considered. For example, coral bleaching and associated mortality may selectively remove faster growing taxa, resulting in less rapid $CaCO_3$ accretion and more rapid net removal of framework material by bioerosion (56, 59). In many locations, coral reefs act as barriers that protect coastlines from incident wave energy; a change in reef depth could alter the coastal energy regime and erosion patterns (116). Over the next several decades these possibilities are likely to be significant only in

particularly vulnerable locations (e.g. low islands) or in association with extreme events such as storms.

Carbonate Mineral Saturation State

A major feature of coral reefs is the precipitation of substantial quantities of $CaCO_3$ from the overlying water, thus modifying the chemical balance of the local marine CO_2 system. One of the best characterized human perturbations of the global climate system is the rate of CO_2 emission to the atmosphere and consequent changes of atmospheric CO_2 content. Changes in atmospheric CO_2 are well documented over the past several decades, reasonably well estimated over at least the last 150 years, understood in broad outline over the past 160,000 years, and at least semi-quantitatively predictable over the next century (78, 136). Estimates of increased atmospheric CO_2 invasion into the upper ocean are much modeled and discussed. While there is uncertainty on the quantity of CO_2 invasion into the ocean, it is reasonably well understood in comparison to other aspects of the global carbon budget (16, 150).

It is well established that the average CO_2 partial pressure (pCO_2) of surface ocean waters has remained within 10–20 μatm of the pCO_2 of the atmosphere as a result of CO_2 mass transfer across the air-sea interface. It seems likely that, as atmospheric pCO_2 continues to rise above the present level of about 350 μatm, the average partial pressure difference between the air and surface ocean will remain small. This increase in pCO_2 will change carbonate mineral saturation states, as outlined in the following discussion.

Consider tropical seawater (salinity = 35‰, temperature = 25°, total alkalinity = 2.3 meq/liter, and present pCO_2 = 350 μatm). It can be calculated (111, 120, 134) that seawater of this composition is about 520% saturated with respect to the common $CaCO_3$ mineral calcite; 340% saturated with respect to aragonite (the most common form of carbonate on coral reefs, deposited by reef-building corals and calcareous green algae); and 260% saturated with respect to 15 mol% Mg-calcite (commonly precipitated by coralline red algae, echinoderms, and many other reef taxa). With increasing Mg substitution for Ca in the calcite, mineral solubility increases, and saturation state of the water with respect to that mineral decreases. A 1–2° temperature increase (about what is predicted for tropical surface seawater over the next century) would not shift saturation states much, but a pCO_2 increase to 600 μatm (again, about what is expected) would decrease the saturation states with respect to the above minerals to about 360%, 240%, and 190%, respectively.

Despite the obvious potential for a link between oceanic CO_2 composition and the process of calcification, there is very limited information about the responses of reef organisms to changes in carbonate saturation state. Studies by Agegian (1), with portions also summarized in Mackenzie & Agegian,

1989 (107), Borowitzka (13), and Smith & Roth (135) on coralline algal growth in response to changes in the aqueous CO_2 system give discrepant results. Data by both Agegian and Borowitzka tend to indicate inhibition of algal growth by high pCO_2, while data by Smith & Roth show accelerated growth at least to modest levels of CO_2 elevation. The former results seem to us to be more plausible as long-term sustained phenomena. Yamazato (166) found that the growth rate of the coral *Fungia scutaria* varied as a function of Ca^{++} concentration in short-term experiments; this effect could result from altered saturation state.

A related issue is potential CO_2 fertilization effects on marine organic productivity. A doubling of atmospheric CO_2 has the potential to increase the photosynthesis of some macroalgae and seagrasses by a factor of two, and that of entire marine communities by up to 20% (159). Coral reef turf algal assemblages have productivity responses to altered pH that are consistent with the predicted fertilization effects of dissolved CO_2 (67). The response of calcifying algae or symbiotic corals to increasing pCO_2 may depend on whether tissue growth or calcification is the rate-limiting step in a given location. At the community level, the combination of photosynthetic enhancement and possible calcification reduction could enhance the competitive advantage of algal communities relative to coral communities, an effect that would be reinforced by community responses to nutrient loading (discussed below).

If we assume that, over time, calcification of many reef organisms will be generally proportional to carbonate mineral saturation state, we can postulate how reef ecosystems might respond to decreasing $CaCO_3$ saturation state. As calcification decreases, the ability of reefs to keep up with rising sea level may diminish. Alternatively, skeletal density may decrease, leaving the organisms more vulnerable to physical damage or bioerosion. The mineralogy of calcifying organisms may shift toward the less soluble mineral phases. Community structure may shift as noncalcifying organisms and bioeroders outcompete calcifying organisms. Habitat provided by corals for other organisms may become restricted.

We clearly know too little about the links between atmospheric CO_2, marine benthic productivity, and marine calcification; and available information is partially contradictory. Growth-rate and metabolic experiments that carefully and explicitly define and control aqueous CO_2 chemistry are required, and the experimental data will then require thoughtful extrapolation to environmentally relevant time scales.

Temperature

Unusually elevated water temperature is a stressor that commonly leads to bleaching (see discussion above) of corals and some other zooxanthellate

organisms, and it will result in death if the "dose" (excess temperature times duration of excursion) is great enough. This factor is of particular concern because it is one of the few climate-related variables that has the potential for extensive near-term damage to coral reef communities (17). Temperature sensitivities of Indo-Pacific corals have been reviewed (86).

Temperature sensitivity in corals is clearly adaptational; the vulnerability of corals in a given locale varies by taxon and is related to the long-term historical record of mean temperature of the warmest month at that site (86). Temperature-induced bleaching can occur in response to 1–2 day exposures to temperatures 3–4° above the normal maximum, or to several weeks of exposure to elevations of 1-2°. Mortality is > 90% for temperature elevations in excess of 4° for periods as short as even a few hours (26), while relatively prompt recovery is the norm for bleaching episodes induced by temperature excursions < 2°.

Temperature responses of some coral symbionts, parasites, and co-occurring organisms appear similar to those of the hosts (60, 86). Bleaching in other symbiotic reef taxa (Millepora, soft corals, zoanthids) (82) also appears to be induced by elevated temperatures, but symbiotic sponges show less propensity for thermal bleaching (153). Irradiance (either visible or UV) may be interactive with elevated temperature in producing stress (86, 99, 129).

Systematic studies of coral temperature responses have been carried out independent of the bleaching issue for corals from tropical and subtropical locations (86). Calcification, P:R values, reproduction, and recruitment all showed maximum values near the local average maximum temperature (about 27° for Hawaii and 31° at Enewetak), with significant reductions at temperatures as little as 1–2° higher. From the standpoint of community response to temperature, these data need to be considered in view of a number of other observations (86): (i) At a given location a significant range of temperature responses appears among different colonies of the same species, and there may be systematic differences between intraspecific types or clones, or between microenvironments (28); (ii) there are systematic differences between species—those with the highest respiratory rates are more sensitive to elevated temperature, and branching species (especially Acropora and Pocillopora) are more vulnerable than massive corals (e.g. Porites); (iii) individual colonies have not been observed to exhibit temperature acclimation on time scales of months to years (86); and (iv) temperatures of 33–34° are tolerated by apparently healthy coral communities in the Great Barrier Reef (89) and the Arabian Gulf (23), where some species survive temperatures of 36–38°. However, recent observations in the Arabian Gulf indicate that even corals adapted to unusually high ambient temperatures remain susceptible to bleaching and other lethal or sublethal responses to slight additional temperature elevations (59, 128).

These observations indicate that reef ecosystem responses to rising temperature will be very dependent on the time scales of change and on other local environmental conditions. An increase in sea surface temperature or its variability, characterized primarily by increasing frequency of sublethal stress or partial mortality and occurring on time scales of the same magnitude as coral generation times, will probably tend to shift coral communities toward heat-tolerant "ecotypes" or species. More extreme temperature excursions or more rapid increases in mean water temperature could result in rapid change of reef diversity and community structure through extensive mortality and species-selective inhibition of reproduction and recruitment. The probability of local extirpations or total extinctions (58, 61) or of failure of reef communities to recover after thermal mortality (56, 60) would depend not only on the rate of change of mean temperatures, but also on the geographic distributions of extreme events and on other environmental controls on reef development.

In view of the fundamental importance of temperature sensitivity to questions of reef response to global change, we suggest that priority should be given to further research into the rates and mechanisms of organism and community adaptation, into the genetic and physiologic bases for thermal sensitivity, and into synergism or interactions between elevated temperature and other potential stressors. A particularly important avenue of research may relate to the question of the nature and distribution of strains or species of zooxanthellae (125). If temperature or stress response of the host-symbiont pair is influenced by algal as well as by coral genetics, and if multiple strains of algae are present in a given locale, then bleaching and reinfection could provide a mechanism for rapid adaptive change.

Visible and Ultraviolet Light

Corals have light requirements and adaptive mechanisms such that maximum rates of calcification and photosynthesis can be sustained to depths of as much as 20 m in clear water (52). Symbiotic corals occur to depths in excess of 60 m, albeit with much reduced rates of growth (80). The depth distribution of light, interacting with other environmental variables such as wave energy, is believed to account for such important reef characteristics as a broad maximum in biodiversity between 10 and 30 m (80) and maximum rates of reef accretion between 5 and 15 m (77).

Although high light levels do not appear to induce stress in corals if other environmental factors are optimal, they enhance coral sensitivity to temperature- and salinity-induced stress (86) and have been implicated as a factor in some episodes of coral bleaching (see discussion above). Photoinhibition appears to occur only at very shallow depths (80).

There are no anticipated climate or environmental changes that would

increase peak clear-day visible light irradiance values. Net annual or seasonal irradiance incident on a reef community, and therefore the incidence of light-related stress and the depth range of optimal growth, could change in response to systematic changes in sea state, cloud cover, or turbidity (55). Cloud cover is one of the most poorly understood and poorly modeled features of the Greenhouse climate (30), and changes in surface wind fields (which influence light penetration by controlling surface roughness) are also not predictable at present. Increases in turbidity can result from input of suspended terrigenous sediments, or from planktonic primary production stimulated by nutrient loading. Both sedimentation and nutrient loading (see discussions below) tend to be anthropogenic stresses resulting from land use, population density, and resource exploitation (49, 105, 109, 142). Extreme turbidity can also occur from resuspension of naturally produced and trapped carbonate particles in restricted reef lagoonal environments (126).

Although not climatic in the narrowest definition of the term, the expected increase in ultraviolet-B (UVB) radiation levels due to destruction of the stratospheric ozone layer by chlorofluorocarbons may be significant; the factors controlling UVB penetration in the water column are the same as for visible light. Detrimental effects on coral reef fauna have been documented (85, 88, 133), and some of the mechanisms identified (99). UV levels in shallow water are clearly able to inhibit photosynthesis (102, 137, 163, 164). The depth-dependent occurrence of UV-blocking pigments in corals has been demonstrated (87, 88), as have photoadaptation and UV tolerance in specific strains of zooxanthellae (87, 88, 98).

Reproduction of reef organisms may also be affected by increased UV levels, either directly or through mortality of planula larvae. There are no data on these specific effects on reef organisms, but studies of mature and larval zooplankton (33, 37) indicate a wide range of UVB sensitivities, with at least some organisms vulnerable to present or increased UV levels in the near-surface environment.

Concern about the possible effects of increased UVB exposure is somewhat tempered by the fact that predicted increases in the tropics are relatively small; average low-latitude UVB surface exposures are expected to increase by 1–10%. This estimate is based on average ozone column depletion estimates of 0.5–5.0% (depending on the trace gas scenario used), although with the potential for much larger local variations (48), and an approximate UVB surface exposure increase of twice the ozone column depletions (165). However, lack of knowledge about UVB exposure effects, especially related to reproduction, combined with recognition that some organisms are sensitive at present levels, indicates that this topic merits further research.

On an overall basis, the present-day distribution of coral reefs across a range of light and water-clarity regimes suggests that changes in light availability

and UVB exposure will probably be secondary factors in determining the response of coral reef systems to regional climate or local anthropogenic change. We note that visible light and UVB may be coincident contributors to reef stress under conditions of clear skies, calm water, and elevated temperature (86, 99, 129), but that in general the factors (cloudiness, sea level rise, turbidity) that reduce levels of desirable light exposure also protect against the deleterious effects of UVB. Because of the characteristics of light extinction with depth and the nature of community and organism adaptation, reduction of exposure levels will have little negative effect on shallow communities but may be deleterious to deeper ones; increased exposures may increase stress levels on shallow reefs but improve conditions at depth.

Currents, Waves, and Storms

Circulation exerts primary control over the distributions of salinity, temperature, nutrient levels, etc. by water mass advection and by determining the intensity and locations of upwelling, and secondary control of nutrient, sediment, and contaminant distributions by interacting with local (often anthropogenic) sources. Distributions of reefs and related or competing communities are controlled to a significant degree at the large and intermediate spatial scales by advective transport of propagules (3). The propagation of pathogens at the regional level has also been identified with major circulation patterns (100). Zonation, reef morphology, and the depth distributions of reef corals, algae, and other key organisms are strongly influenced by physical factors, including wave action (41, 80). Storms, waves, and currents are also the driving forces for sediment transport, coastal dynamics and geomorphology, and local relative sea level. Local circulation effects will interact with those of sea level rise, and in some significant cases they may be controlled primarily by sea level rise (see discussion above).

As with other factors, generalization about the effects of climate change on physical oceanography is difficult because specific effects will be regional or local in nature and because we lack adequate predictions about probable changes at those scales. In addition to modifications to the patterns mentioned above, there are specific reef-related issues: (i) Upwelling is an important local circulation phenomenon on several reef systems (83, 96, 162). It has been suggested that in some locations both the frequency and the intensity of temperate-latitude coastal upwelling may be significantly altered by changing weather conditions (4). The regional resolution of general circulation models is insufficient to predict how upwelling might change in specific reef settings. (ii) Storms provide long-term episodic control of reef community development by catastrophic pruning and/or substrate renewal (40, 72). In some instances, such disruption aids in coral reproduction (74). Storms influence community succession and diversity directly at the local level (74). Storm

frequencies and/or intensities may increase under warmer conditions, but geographic distributions may shift; the result will be long-term shifts in community succession and development patterns in reefs subject to changed disturbance regimes.

Sedimentation

Sedimentation is not primarily a climatic factor, although natural coastal erosion and sediment accumulation patterns may alter as a result of changing currents, sea level, wave energy, or storm patterns. More significant factors are likely to be land use (e.g. deforestation, agricultural practices, dredging, coastal construction—158). The stress-related aspects of sedimentation have been reviewed by Brown & Howard (18) and Grigg & Dollar (66).

Rapid sedimentation can smother corals and other sedentary reef organisms (49, 109); slower but significant rates of sedimentation as well as high rates of sediment resuspension are known to cause reductions in coral growth rate (2, 38, 39, 105, 108, 117). It should be kept in mind, however, that coral morphology as well as sediment grain size affects the ability of coral colonies to cleanse themselves of sediment (79, 168). As a result, community structure will be altered by changing sedimentation regimes. Occlusion of hard substrate with soft sediment can reduce coral recruitment (12, 75). Increased sedimentation is often, but not always, accompanied by elevated turbidity and nutrient levels (discussed below). Among the mechanisms for deleterious effects are choking of feeding mechanisms, sulfide generation, prolonged contact with toxic components of the sediment, and facilitation of bacterial "infections" (18, 66).

Salinity

Although most reef systems occur near the apparently optimal salinity value of about 35 ‰, many reefs can be found in localities that show significant variations in mean or extreme salinities. It is therefore possible to extract considerable information about reef responses to salinity from natural distribution patterns.

Coles & Jokiel (25) have reviewed field and laboratory data on the responses of corals and other reef organisms to salinity, and they report that natural reef communities seem to do well within a salinity range of about 25–40 ‰, with rapid loss of taxa at higher salinities. Salinity maintained below 20 ‰ for longer than 24 hours is lethal for corals and most other reef taxa (49, 151). The lethal response is more rapid at lower salinities. Sublethal responses to salinity excursions include expulsion of zooxanthellae (hence, "bleaching") and altered metabolic rates (24, 114).

Salinity is unlikely to show significant regional-scale shifts of magnitudes that will affect coral reefs during a period of changing climate, but there will

be local alterations of salinity regimes, especially in terms of variability. Local salinity excursions that are primarily associated with slow water exchange will tend to be reduced as sea level rises. Except in very restricted shallow water bodies, evaporation is unlikely to proceed rapidly enough to cause short-term excursions to excessively high salinity values. Salinity depressions are much more probable short-term excursions. Local reef areas adjacent to large or "flashy" drainage basins will be vulnerable to increased flow that will chronically or episodically depress salinity to well below currently observed levels. Such occurrences will have potentially dramatic local impacts on corals and other reef organisms.

Climate-induced changes in local salinity stress may result from shifts in rainfall amount or intensity, but as with sedimentation, a more important factor in populated areas is likely to be changes in runoff pattern resulting from land-use patterns such as urbanization and deforestation.

Nutrients

Inorganic plant nutrients have long been implicated in damage to coral reef communities (71), and increasing human pressures are leading to elevated nutrient discharges from sewage, agricultural practices, and land use. These changes may be the most pervasive human-induced alterations of the coastal zone. Perhaps the most intensively studied example of nutrient effects on coral reefs has been Kaneohe Bay, Hawaii (6, 89, 91, 108, 142, 160). This system received substantial and increasing discharges of sewage-derived nutrients over a 20-year period; the discharge was abruptly terminated in 1977. A particularly noteworthy characteristic of Kaneohe Bay is the degree to which reef communities had recovered several years after termination of sewage discharge into this system (50).

Other major reef systems such as the Australian Great Barrier Reef (167) and the Florida Reef Tract (70) are increasingly discussed in terms of observed or perceived nutrient stress due to anthropogenic activity. Nutrient loading is certainly increasing on many aquatic communities adjacent to growing human populations, particularly in areas where water quality regulations are lax.

The major impact of nutrients on coral reefs usually appears to be indirect. Corals require very little external nutrient supply because of effective internal nutrient recycling between the coral animal host and the zooxanthellae plant symbiont (68, 113). Other taxa of common photosynthetic reef organisms also thrive at low nutrient concentrations. The primary production rate of coral reefs is very high (90) but is almost exactly balanced by the respiration rate (29, 90). Coral reef communities subjected to high nutrient levels appear to undergo deterioration due to overgrowths by filamentous algae, bryozoans, and barnacles, increased plankton-generated turbidity, increased bioerosion, and poor coral recruitment (9, 69, 101). Hallock (69) and Birkeland (11)

have suggested that reef growth diminishes along a gradient from oligotrophic to eutrophic conditions.

However, Kinsey (92) has observed that it is incorrect to jump from the observation that coral reefs can do well under low nutrient conditions to the conclusion that coral reefs require such low nutrient environments. We agree, noting that some reefs look healthy and are apparently doing well in a milieu of naturally high nutrient levels (62, 140). At the organism level, increased nutrients cause increases in both the pigmentation per cell and the absolute number of cells of symbiotic zooxanthellae (47, 112). Although there is no evidence that increased nutrients are a physiological stress in themselves, studies are needed on whether elevated nutrients change the sensitivity of the symbiotic assembly to other stresses, particularly temperature and/or light-induced effects. We suggest that an important consideration for any particular reef community (which may be adapted to a wide range of nutrient regimes) is the rate of change in the nutrient loading into that system and its interaction with other environmental variables.

At the community level, rapid nutrient changes can cause shifts in structure and function. With an increase in nutrients, rapidly growing phytoplankton and benthic algae gain a competitive advantage over corals, often overgrowing and eventually smothering them (6, 11, 66, 69, 142). Turbidity of the water resulting from increased plankton biomass and detritus can also cause reef deterioration (142). (See also discussion of light effects, above). Perhaps an even more important effect is that suspension-feeding animals, especially those that bore into calcareous substrata, become abundant in high nutrient waters replete with particulate organic matter (10, 14, 66, 69, 142, 160). Many of these organisms damage the structural integrity of the reef, and the larvae of sponges, barnacles, ascidians, and other sedentary organisms can outcompete coral larvae for space. High organic loading, which may be associated with some types of nutrient loading, can also kill corals and other organisms because of elevated biochemical oxygen demand and hydrogen sulfide release (66). Nutrient loading may also be associated with reef stress induced by increased sedimentation.

Some evidence suggests direct damage to reef organisms from elevated nutrients. Yamazato (166) reported that high levels of phosphate apparently inhibited coral calcification during incubation experiments. Kinsey & Domm (93) inferred a similar effect for a reef community deliberately fertilized with inorganic phosphorus and nitrogen. Walker & Ormond (154) found localized mortality of corals in the vicinity of sewage discharge and spillage of phosphate dust during ship loading. One might also postulate such direct effects from locally high levels of ammonium. If such direct nutrient-induced mortality does occur, it seems most likely to be associated with very high nutrient concentrations. Such effects could usually be anticipated to be

localized. A "halo" around a discharge site would be inside of a much broader zone, exhibiting the secondary effects we have noted.

Other Anthropogenic Stresses

Anthropogenic environmental alterations, especially those connected with land use and waste disposal, have been discussed in connection with many of the factors considered above. Coral reef stresses have been recently reviewed (18, 66) and cataloged (158). Two classes of anthropogenic stress not previously discussed merit mention.

Toxins introduced into the marine environment may include such materials as oil (18, 84), metals (18, 63, 147), and pesticides (63, 147). Although these have thus far been documented as having only local effects, their obvious association with human population and economic development suggests that they deserve continued attention.

Direct reef resource utilization (quarrying, dredging, harvesting of organisms, tourism) represents a significant threat and a confounding variable when assessing other forms of environmental change. In particular, many coral reefs, especially those adjacent to land masses supporting large human populations, receive fishing pressure sufficient to reduce the population of fishes dramatically (158). Fish grazing is known to be an important control on plant biomass on reefs. Large algal populations are often attributed to excessive nutrient loading; an important alternative interpretation is that fishing pressure has removed those herbivorous fishes that might have grazed on the algae and prevented their excessive growth.

The effects of resource utilization are important to understanding environmental change, both because they can mimic or obscure the effects of climate or other environmental change, and because the utilization tends to exacerbate the effects of the more directly environmental influences discussed above.

"PATHWAYS" OF CLIMATE FORCING

Table 1 presents a slightly modified list of the factors discussed above, subdivided according to whether environmental changes over the next few decades are more likely to result from changing climate or from other anthropogenic environmental alterations.

In order to assess relative importance or sensitivity, these same stressors may be categorized by their primary pathway or mechanism of delivery to the local reef environment. Those factors transmitted primarily through the atmosphere or via air-sea interaction are identified with the atmospheric pathway; the hydrographic pathway corresponds to those features normally associated with physical oceanography, and the hydrologic pathway involves effects transmitted or created through the mechanisms of evaporation,

Table 1   Dominant sources of near-term coral reef stresses

Climate	Other
Sea level rise**	Ultraviolet light**
CO_2 changes**	Nutrients (*?)
Temperature change*	Sedimentation
Visible light	Turbidity
Current/storm change	Toxics
(Fresh water)	Resource use
	(Fresh water)

** global, trends monotonic
* trends in global mean monotonic, significant spatial temporal exceptions

precipitation, runoff, or groundwater flow. This list is given in Table 2; although not rigorous, it provides a basis for identifying signal amplification possibilities.

It seems clear that all three pathways by which changing climate influences aquatic ecosystems will have their major influence in shallow water. From the standpoints of sensitivity, vulnerability, and monitoring, marginal environments are particularly sensitive to change because of their steep gradients and physical constraints. Coastal zones are a particularly good example of such environments, and a large fraction of the world's coral reefs occur within coastal zones or their physical extensions, enclosed and/or shallow basins, or shelf environments. In such locales the hydrologic pathway has a particularly high signal amplification because effects may be integrated over very large land areas and focused (e.g. through runoff) onto the narrow coastal zone. It is important to note that the stressors delivered via the hydrologic pathway are generally those in the "other" (non-climate) source category.

This analysis leads to the conclusion that reefs in proximity to land masses or in relatively shallow or enclosed basins will be particularly sensitive (or vulnerable) to the effects of environmental change but will have a low specificity for climatic variables. In the near term, the suggestion is strong that local and regional effects of population growth, land use, etc, will have

Table 2   Dominant pathways of stress delivery

Atmospheric	Hydrographic	Hydrologic
Temperature	Sea level	Fresh water
		Nutrients
UV light	Currents	Sedimentation
Visible light	Storms/waves	Toxics
CO_2 change		Turbidity

more effect on these reefs than the more distributed and gradual climatic changes. Oceanic reefs are probably more sensitive to the truly climatic component of environmental change and could serve as control sites for studies in the more complex nearshore environment. Stress responses can be observed on a local or regional basis but may represent various categories of response: (i) Direct physiological response of an organism to a single environmental variable such as temperature or light; (ii) interactive responses of organisms to concurrent changes in multiple variables (e.g. temperature plus light, water quality plus light or temperature); and (iii) indirect effects on competitive relationships or community interactions, whether or not accompanied by overt evidence of physiologic stress at the organism level.

We note that chemical stresses are more likely to be observed at the community level, while physical stress is more readily observed in terms of organism response. Indirect effects will be situational and highly variable on a spatial scale. This highlights the problems of scale and variability associated with the use of local reef responses for detection of global signals, "average" ecosystem conditions, or responses to environmental forcing; extensive networks of long-term observations will be required.

DISCUSSION

Large-Scale Issues

On large scales, the environmental effects specifically attributable to climate change would suggest that reefs as a global biotic phenomenon are not seriously threatened. We know that reefs are structurally and functionally similar over a wide range of conditions and dominant species, indicating that the communities are not highly dependent on specific individual taxa and may be resilient to the loss of some more vulnerable species. When we consider individual climatic factors in isolation, we see that the effects of sea level rise on coral reefs over the next century are more likely to be positive than negative. Increases in maximum sea surface temperatures will increase the frequency of temperature-induced stress or mortality events, but increases in minimum and/or average values may extend the geographic range of conditions suitable for reef development on a longer time scale. Climatic changes in hydrologic or hydrographic factors may have positive or negative effects on a local scale. Although we may expect significant changes in the details of reef characteristics and distributions, there is at present no basis for predicting widespread deleterious effects on average. There are two important caveats to this conclusion:

One is that we know remarkably little about the probable effects of increasing UV exposure and of decreasing carbonate saturation state. Although there is no evidence that either one represents a potential near-term cataclysm,

their effects are predominantly negative, their distribution is global, and the nature of change is reasonably predictable. Focussed research is clearly needed.

A more important caveat stems from the artificiality of considering climate-induced stresses by themselves. Reef damage from anthropogenic environmental degradation is widespread, represents a much greater threat than climate change in the near future, and can reinforce negative effects of climate change. In particular, we note that many anthropogenic changes represent chronic stresses that may interfere with reef recovery from the acute stress events that are likely to increase in frequency as a result of climate change. The combination poses threats on a regional level that we believe should be taken seriously. As an example, we note that the Caribbean fits the profile of a vulnerable region: biodiversity is far lower than in the Indo-Pacific; it has been more vulnerable than the Indo-Pacific during past climate fluctuations; it is a relatively enclosed basin with a growing human population in its drainage area and abundant evidence of anthropogenic effects and terrigenous (e.g. runoff-related) influences; there are no other large-scale reef communities in the tropical Atlantic that can serve as refugia or sources of recolonization; and evidence of widely distributed reef stress has already been noted.

Local Issues

At the local level, concerns are about the specific condition of specific reefs, and reassurances on the global average level offer little joy. We gain some additional levels of predictability and impact assessment with a local focus, whereas in a general treatment such as this review we are forced to fall back on generalities and uncertainties. When we look at a specific site we are dealing with known hydrologic, hydrographic, population, and development characteristics; and specific vulnerabilities and probabilities are much more identifiable. The effects of chronic stress and altered disturbance regimes may be effectively evaluated on the local level; Bales (5) points out in a discussion of altered hydrologic regimes that "Human-related disturbances tend to differ from natural disturbances in being more frequent and of different intensity. Systems dominated by human-related disturbances tend to be less diverse biologically. Physically they have less structure and complexity . . . we need to better understand the long-term impacts of altering natural disturbance regimes in order to adequately address such issues as biodiversity and cumulative impacts." However, for some types of acute stress, the scale mismatch becomes more critical—if the effects of climate change are felt (as seems probable) primarily through changes in the frequency and magnitude of extreme events, then effects at small spatial scales can be predicted only on a probabilistic basis. Overall, we suspect that many human populations will, over the next few decades, come to grips with the previously abstract geological truism that individual reefs are transient phenomena.

Scientific Issues

There are critical needs for data on the nature and variability of organism and symbiont responses to specific environmental factors (notably carbonate mineral saturation state, temperature, and UVB), and especially on the combined effects of potentially interacting stresses and environmental conditions such as nutrient loading. There are enormous challenges ahead in learning how to relate observations, theory, and predictions across differing time and space scales; this has been identified as one of the highest priorities for research in hydrology (115), which has been pointed out above as an extremely sensitive pathway for the effects of environmental or climate change.

The human race appears to be in the process of conducting an unplanned planetary experiment in what might be loosely termed accelerated evolution. If the scientific community has the resolve and insight necessary to discern and take advantage of the "design" inherent in this experiment, there is enormous understanding to be gained—much of it vitally useful to society in preparing for or responding to the unintended consequences of our experiment.

Institutional Issues

Addressing the various needs and opportunities will require significant changes in our present scientific culture and institutional structures. One of the greatest administrative challenges is the need for funding and research institutions to develop an effectively coordinated approach to problems that have time scales in excess of budget cycles and political administration lifetimes, and both spatial scales and ranges of implications that transcend academic disciplines, agency missions, and geopolitical boundaries (15, 21).

A specific focus of the administrative problem is the need for long-term, globally integrated, and stable yet technically evolving data acquisition programs. The traditional term is monitoring, and the traditional attitude among researchers is that "monitoring" is an activity of dubious merit, particularly if it competes with "research" for resources. At the time and space scales of global change, however, there is no basis for this dichotomy. Monitoring is an intrinsic and essential part of research (32), and its design and effective conduct should be one of the highest priorities of the research community, because our ability to formulate and test hypotheses will depend on the data bases available. Retrospective extension of monitoring observations by integrating paleoecological and neoecological studies will be an important component of efforts to extend our baseline data both temporally and spatially.

Finally, we note (not for the first time) that the scientific culture will need to find ways for better integration across disciplinary boundaries as well as across time and space scales within disciplines. Reef research has long been dominated by biologists and geologists, yet climate and stresses induced by climate change are defined and studied in physical and chemical terms. A

concerted effort to match studies of physical/chemical forcing functions with the biological/geological responses appears to us to be the only way to synthesize an effective approach to global change issues.

Literature Cited

1. Agegian, C. R. 1985. *The biogeochemical ecology of Porolithon gardineri (Foslie)*. PhD thesis. Univ. Hawaii, 178 pp.

2. Aller, R. C., Dodge, R. E. 1974. Animal-sediment relations in a tropical lagoon—Discovery Bay, Jamaica. *J. Mar. Res.* 32:209–32

3. Andrews, J. C., Pickard, G. L. 1990. The physical oceanography of coral-reef systems. See Dubinsky 1990, pp. 11–48

4. Bakun, A. 1990. Global climate change and intensification of coastal ocean upwelling. *Science* 247:198–201

5. Bales, R. C. 1991. Hydrology sessions at the 1990 fall AGU meeting. EOS, Transactions, Am. Geophys. Union 72:243

6. Banner, A. H. 1975. Kaneohe Bay, Hawaii: Urban pollution in a coral reef ecosystem. *Proc. 2nd Int. Symp. Coral Reefs, Brisbane* 2:685–702

7. Bard, E., Hamelin, B., Fairbanks, R. G., Zindler, A. 1990. Calibration of the ^{14}C timescale over the past 30,000 years using mass spectrometric U-Th ages from Barbados corals. *Nature* 345: 405–10

8. Barnes, D. J., Lough, J. M. 1989. The nature of skeletal density banding in scleractinian corals: Fine banding and seasonal patterns. *J. Exp. Mar. Biol. Ecol.* 126:119–34

9. Birkeland, C. 1977. The importance of rate of biomass accumulation in early successional stages of benthic communities to the survival of coral recruits. *Proc. Third Int. Coral Reef Symp., Miami.* 1:16–21

10. Birkeland, C. 1987. Nutrient availability as a major determinant of differences among hard-substratum communities in different regions of the tropics. In *Differences between Atlantic and Pacific Tropical Marine Coastal Ecosystems: Community Structure, Ecological Processes, and Productivity*, ed. C. Birkeland, pp. 45–90. Paris: UNESCO

11. Birkeland, C. 1988. Geographic comparisons of coral-reef community processes. *Proc. 6th Coral Reef Symp., Townsville* 1:211–20

12. Birkeland, C., Rowley, D., Randall, R. H. 1982. Coral recruitment patterns at Guam. *Proc. Fourth Int. Coral Reef Symp., Manila* 2:339–44

13. Borowitzka, M. A. 1981. Photosynthesis and calcification in the articulated coralline alga *Amphiroa anceps* and *A. foliaceae. Mar. Biol.* 62:17–23

14. Brock, R. E., Smith, S. V. 1983. Response of coral reef cryptofaunal communities to food and space. *Coral Reefs* 1:179–93

15. Broecker, W. S. 1987. Unpleasant surprises in the greenhouse? *Nature* 328: 123–26

16. Broecker, W. S., Takahashi, T., Simpson, H. J., Peng, T.-H. 1979. Fate of fossil fuel carbon dioxide and the global carbon budget. *Science* 206:406–18

17. Brown, B. E. 1990. Coral bleaching: special issue. *Coral Reefs* 8:153–232

18. Brown, B. E., Howard, L. S. 1985. Assessing the effects of "stress" on reef corals. *Adv. Mar. Biol.* 22:1–63

19. Brown, B. E., Suharsono 1990. Damage and recovery of coral reefs affected by El Niño related seawater warming

in the Thousand Islands. Indonesia. *Coral Reefs* 8:163–70

20. Buddemeier, R. W., Kinzie, R. A. III 1976. Coral growth. *Oceanogr. Mar. Biol. Ann. Rev.* 14:183–225

21. Buddemeier, R. W., Smith, S. V. 1988. Coral reef growth in an era of rapidly rising sea level: Predictions and suggestions for long-term research. *Coral Reefs* 7:51–56

22. Bunkley-Williams, L., Williams, E. H. 1990. Global assault on coral reefs. *Nat. Hist.* 4:47–54

23. Coles, S. L. 1988. Limitations on reef coral development in the Arabian Gulf: temperature or algal competition. *Proc. 6th Int. Coral Reef. Symp., Townsville* 3:211–16

24. Coles, S. L., Jokiel, P. L. 1978. Synergistic effects of temperature, salinity and light on the hermatypic coral *Montipora verrucosa. Mar. Biol.* 49: 187–95

25. Coles, S. L., Jokiel, P. L. 1992. Effects of salinity on coral reefs. In *Pollution in Tropical Aquatic Systems*, ed. D. Connell, D. Hawker. Boca Raton, Fla: CRC. In press

26. Coles, S. L., Jokiel, P. L., Lewis, C. R. 1976. Thermal tolerance in tropical versus subtropical Pacific reef corals. *Pac. Sci.* 30:159–66

27. Connell, J. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199:1302–10

28. Cook, C. B., Logan, A., Ward, J., Luckhurst, B., Berg, C. J. Jr. 1990. Elevated temperatures and bleaching on a high-latitude coral reef: the 1988 Bermuda event. *Coral Reefs* 9:45–49

29. Crossland, C. J., Hatcher, B. G., Smith, S. V. 1991. Role of coral reefs in global ocean production. *Coral Reefs* 10:55- 64

30. Cubasch, U., Cess, R. D. 1990. Processes and modeling. In *Climate Change: The IPCC Assessment*, ed. J. T. Houghton, G. J. Jenkins, J. J. Ephraums, pp. 69–92. Cambridge: Cambridge Univ. Press

31. Cubit, J. D. 1985. Possible effects of recent changes in sea level on the biota of a Caribbean reef flat and predicted effects of rising sea levels. *Proc. Fifth Int. Coral Reef Congr., Tahiti* 3:111–18

32. D'Elia, C. F., Buddemeier, R. W., Smith, S. V. 1991. *Workshop on Coral Bleaching, Coral Reef Ecosystems and Global Change: Report of Proceedings. Maryland Sea Grant Coll. Publ. No. UM-SG-TS-91–03.* College Park, Md: Univ. Maryland

33. Damkaer, D. M., Dey, D. B. 1983. UV damage and photo-reactivation potentials of larval shrimp, Pandalus platyceros, and adult euphausiids, *Thysanoessa raschii. Oecologia* 60:169–75

34. Davies, P. J. 1988. Evolution of the Great Barrier Reef - reductionist dream or expansionist vision. *Proc. Sixth Int. Coral Reef Symp., Townsville* 1:9–17

35. Davies, P. J., Hopley, D. 1983. Growth facies and growth rates of Holocene reefs in the Great Barrier Reef. Bur. Mineral Resources. *J. Aust. Geol. Geophys.* 8:237–51

36. Davies, P. J., Marshall, J. F., Hopley, D. 1985. Relationship between reef growth and sea level in the Great Barrier Reef. *Proc. Fifth Int. Coral Reef Congr., Tahiti.* 3:95–103

37. Dey, D. B., Damkaer, D. M., Heron, G. A. 1988. UV-B dose/dose-rate responses of seasonally abundant copepods of Puget Sound. *Oecologia* 76: 321–29

38. Dodge, R. E., Aller, R. C., Thomson, J. 1974. Coral growth related to resuspension of bottom sediments. *Nature* 247:547–77

39. Dodge, R. E., Vaisnys, J. R. 1977. Coral populations and growth patterns: responses to sedimentation and turbidity associated with dredging. *J. Mar. Res.* 35:715–30

40. Dollar, S. J. 1982. Wave stress and coral community structure in Hawaii. *Coral Reefs* 1:71–81

41. Done, T. J. 1983. Coral zonation: Its nature and significance. In *Perspectives on Coral Reefs*, ed. D. J. Barnes, pp. 107–47. Manuka, Aust: Brian Clouston

42. Done, T. J. 1987. Simulation of the effects of outbreaks of Crown-of-Thorns starfish on massive corals in the genus Porites: Evidence of population resilience? *Coral Reefs* 6:75–90

43. Done, T. J. 1991. The debate continues—robust versus fragile reefs. *Reef Encounter* 9:5–7

44. Done, T. J. 1992. Phase changes in coral reefs. *Hydrobiologia.* In press

45. Druffel, E. R. M. 1985. Detection of El Niño and decade time scale variations of sea surface temperature from banded coral records: Implications for the carbon dioxide cycle. In *The Carbon Cycle and Atmospheric CO_2: Natural Variations Archean to Present*, ed. E. T. Sundquist, W. S. Broecker. Washington, DC: Am. Geophys. Union

46. Druffel, E. R. M., Dunbar, R. B., Wellington, G. M., Minnis, S. A. 1990. Reef-building corals and identification of ENSO warming periods. In *Global*

Ecological Consequences of the 1982–83 El Niño-Southern Oscillation, ed. P. W. Glynn, pp. 233–53. New York: Elsevier Oceanography Series 52

46a. Dubinsky, Z. 1990. *Coral Reefs: Ecosystems of the World 25.* New York: Elsevier

47. Dubinsky, Z., Stembler, N., Ban-Zion, M., McCloskey, L. R., et al. 1990. The effect of external nutrient resources on the optical properties and photosynthetic efficiencies of *Stylophora pistilleta. Proc. R. Soc. Lond., Ser. B* 239:231–46

48. Eckman, R. S., Pyle, J. A. 1989. Numerical modelling of ozone perturbations. In *Ozone Depletion: Health and Environmental Consequences,* ed. R. R. Jones, T. Wigley, pp. 27–42. New York: Wiley

49. Edmondson, C. H. 1928. The ecology of an Hawaiian coral reef. *Bernice P. Bishop Museum Bull.* 45:64

50. Evans, C. W., Maragos, J. E., Holthus, P. F. 1986. Reef corals in Kaneohe Bay: Six years before and after termination of sewage discharge (Oahu, Hawaii Archipelago). *Univ. Hawaii Inst. Mar. Biol., Tech. Rep. 37.* Kaneohe, Hawaii

51. Fairbanks, R. G. 1989. A 17,000 year glacio-eustatic sea level record. *Nature* 342:637–42

52. Falkowski, P. G., Jokiel, P. L., Kinzie, R. A. III 1990. Irradiance and corals. See Dubinsky, pp. 89–107

53. Fitt, W. K., Spero, H. J., Halas, J., White, M. W., Porter, J. W. 1992. Recovery patterns of the coral *Montastrea annularis* after the 1987 "bleaching event" in the Florida Keys. *Coral Reefs.* In press

54. Flohn, H., Kapala, A., Knoche, H. R., Machel, H. 1990. Recent changes of the tropical water and energy budget and of mid-latitude circulations. Abstracts. *Int. TOGA Sci. Conf.* Honolulu, Hawaii (unnumbered)

55. Glynn, P. W. 1977. Coral growth in upwelling and nonupwelling areas off the Pacific coast of Panama. *J. Mar. Res.,* 35:567–85

56. Glynn, P. W. 1988. El Niño-southern oscillation 1982–83: Nearshore population, community and ecosystem. *Annu. Rev. Ecol. Syst.* 19:309–45

57. Glynn, P. W. 1990. Coral mortality and disturbances to coral reefs in the tropical Eastern Pacific. In *Global Ecological Consequences of the 1982–1983 El Niño-Southern Oscillation,* ed. P. W. Glynn, pp. 55–126. New York: Elsevier Oceanography Ser.

58. Glynn, P. W. 1991. Coral reef bleaching in the 1980's and possible connections with global warming. *Trends Ecol. Evol.* 6:175–79

59. Glynn, P. W. 1992. Coral reef bleaching: ecological perspectives. *Coral Reefs.* In press

60. Glynn, P. W., D'Croz, L. 1990. Experimental evidence for high-temperature stress as the cause of El Niño–coincident coral mortality. *Coral Reefs* 8:181–92

61. Glynn, P. W., de Weert, W. H. 1991. Elimination of two reef-building hydrocorals following the 1982–83 El Niño warming event. *Science* 253:69–71

62. Glynn, P. W., Stewart, R. H. 1973. Distribution of coral reefs in the Pearl Islands (Gulf of Panama) in relation to thermal conditions. *Limnol. Oceanogr.* 18:367–79

63. Glynn, P. W., Szmant, A. M., Corcoran, E. F., Cofer-Shabica, S. V. 1989. Condition of coral reef cnidarians from the northern Florida reef tract: Pesticides, heavy metals, and histopathological examination. *Mar. Poll. Bull.* 20: 568–76

64. Goreau, T. J. 1990. Coral bleaching in Jamaica. *Nature* 343:417

65. Grassle, J. F. 1973. Variety in coral reef communities. In *Biology and Geology of Coral Reefs,* ed. O. A. Jones, R. Endean, pp. 247–68. New York: Academic Press

66. Grigg, R. W., Dollar, S. J. 1990. Natural and anthropogenic disturbance on coral reefs. See Dubinsky, pp. 439–52

67. Hackney, J. M., Sze, P. 1988. Photorespiration and productivity rates of a coral reef algal turf assemblage. *Mar. Biol.* 98:483–92

68. Hallock, P. 1981. Algal symbiosis: a mathematical analysis. *Mar. Biol.* 62: 249–55

69. Hallock, P. 1988. The role of nutrient availability in bioerosion: consequences to carbonate buildups. *Palaeogeogr., Palaeoclimat., Palaeoecol.* 63:275–91

70. Hallock, P. 1990. Coastal pollution and coral communities. *Bull. Am. Littoral Soc.* 19:15–18

71. Hallock, P., Schlager, W. 1986. Nutrient excess and the demise of coral reefs and carbonate platforms. *Palaios* 1:389–98

72. Harmelin-Vivien, M. L., Laboute, P. 1986. Catastrophic impact of hurricanes on outer reef slopes in the Tuamotu (French Polynesia). *Coral Reefs* 5:55–62

73. Heymsfield, A. J., Miloshevich, L. M.

1991. Limit to greenhouse warming? *Nature* 351(2 May 1991):14–15

74. Highsmith, R. C. 1982. Reproduction by fragmentation in corals. *Mar. Ecol. Prog. Ser.* 7:207–26

75. Hodgson, G. 1990. Sediment and the settlement of larvae of the reef coral *Pocillopora damicornis*. *Coral Reefs* 9:41–43

76. Hoegh-Guldberg, O., Smith, G. J. 1989. Light, salinity, and temperature and the population density, metabolism, and export of zooxanthellae from *Stylophora pistillata* and *Seriatopora hystrix*. *J. Exp. Mar. Biol. Ecol.* 129:279–303

77. Hopley, D., Kinsey, D. W. 1988. The effects of a rapid short-term sea level rise on the Great Barrier Reef. In *Greenhouse: Planning for Climate Change*, ed. G. I. Pearman, pp. 189–201. New York: Brill

78. Houghton, J. T., Jenkins, G. J., Ephraums, J. J., eds. 1990. *Climate Change: The IPCC Assessment.* Cambridge Univ. Press: Cambridge

79. Hubbard, J. A., Pocock, Y. P. 1972. Sediment rejection by recent scleractinian corals: a key to paleo-environmental reconstruction. *Geol. Rundsch. (Sonderdr.)* 61:598–626

80. Huston, M. A. 1985. Patterns of species diversity on coral reefs. *Annu. Rev. Ecol. Syst.* 6:149–77

81. Isdale, P. 1984. Fluorescent bands in massive corals record centuries of coastal rainfall. *Nature* 310:578–79

82. Jaap, W. C. 1988. The 1987 zooxanthellae expulsion event at Florida reefs. In *Mass Bleaching of Corals in the Caribbean: a Research Strategy. Research Report 88–2.*, ed. J. Ogden, R. Wicklund, pp. 24–29. Rockville, Md: NOAA Undersea Res. Prog.

83. Jablonski, D. 1991. Extinctions: A paleontological perspective. *Science* 253:754–57

84. Jackson, J. B. C. 1989. Ecological effects of a major oil spill on Panamanian coastal marine communities. *Science*, 243:37–44

85. Jokiel, P. L. 1980. Solar ultraviolet radiation and coral reef epifauna. *Science* 207:1060–71

86. Jokiel, P. L., Coles, S. J. 1990. Response of Hawaiian and other Indo-Pacific reef corals to elevated temperature. *Coral Reefs* 8:155–62

87. Jokiel, P. L., York, R. H., Jr. 1984. Importance of ultraviolet radiation in photoinhibition of microalgal growth. *Limnol. Oceanogr.* 29:192–99

88. Jokiel, P. L., York, R. H. J. 1982. Solar ultraviolet photobiology of the reef coral *Pocillopora damicornis* and symbiotic zooxanthellae. *Bull. Mar. Sci.* 32:301–15

89. Kinsey, D. W. 1979. *Carbon turnover and accumulation by coral reefs.* PhD thesis. Univ. Hawaii. 284 pp.

90. Kinsey, D. W. 1985. Metabolism, calcification and carbon production: System level studies. *Proc. Fifth Int. Coral Reef Congr., Tahiti.* 4:505–26

91. Kinsey, D. W. 1988. Coral reef system responses to some natural and anthropogenic stresses. *Galaxea* 7:113–28

92. Kinsey, D. W. 1991. The coral reef: an owner-built, high-density, fully-serviced, self-sufficient housing estate in the desert—or is it? *Symbiosis* 10:1–22

93. Kinsey, D. W., Domm, A. 1974. Effects of fertilization on a coral reef environment—primary production studies. *Proc. Second Int. Coral Reef Symp., Brisbane.* 1:49–52

94. Kinsey, D. W., Hopley, D. 1991. The significance of coral reefs as global carbon sinks—response to greenhouse. *Paleogeogr., Paleoclimatol., Paleoecol.* (Global and Planetary Change Section) 89:363–77

95. Lapointe, B. E. 1989. Caribbean coral reefs: Are they becoming algal reefs? *Sea Frontiers* 35:82–91

96. Lapointe, B. E., Smith, N. P. 1987. A preliminary investigation of upwelling as a source of nutrients to Looe Key National Marine Sanctuary. *NOAA Technical Memorandum NOS MEND*, 9:53

97. Lasker, H. R., Coffroth, M. A. 1991. Population dynamics and genetic population structure of a Gorgonian coral: Do multi-year studies characterize longer time scale dynamics? *Am. Zool.* 31(5):48A

98. Lesser, M. P., Shick, J. M. 1989a. Effects of irradiance and ultraviolet radiation on photoadaptation in the zooxanthellae of *Aiptasia pallida:* primary production, photoinhibition, and enzymic defenses against oxygen toxicity. *Mar. Biol.* 134:129–41

99. Lesser, M. P., Stochaj, W. R., Tapley, D. W., Shick, J. M. 1990. Bleaching in coral reef anthozoans: Effects of irradiance, ultraviolet radiation, and temperature on the activities of protective enzymes against active oxygen. *Coral Reefs* 8:225–32

100. Lessios, H. A. 1988. Mass mortality of *Diadema antillarum* in the Caribbean: What have we learned? *Annu. Rev. Ecol. Syst.* 19:371–93

101. Littler, M. M., Littler, D. S. 1984. Models of tropical reef biogenesis: the

contribution of algae. *Prog. Phycol. Res.* 3:323–64

102. Lorenzen. D. J. 1979. Ultraviolet radiation and phytoplankton photosynthesis. *Limnol. Oceanogr.* 24:1117–20

103. Lough, J. M., Barnes, D. J. 1990a. Possible relationships between environmental variables and skeletal density in a coral colony from the central Great Barrier Reef. *J. Exp. Mar. Biol.* 134:221–41

104. Lough, J. M., Barnes, D. J. 1990b. Intra-annual timing of density band formation of Porites coral from the central Great Barrier Reef. *J. Exp. Mar. Biol. Ecol.* 135:35–37

105. Loya, Y. 1976. Effects of water turbidity and sedimentation on the community structure of Puerto Rican corals. *Bull. Mar. Sci.* 26:450–66

106. MacCracken, M. C., Budyko, M. I., Hecht, A. D., Izrael, Y. A., ed. 1990. *Prospects for Future Climate: A Special US USSR Report on Climate and Climate Change.* Chelsea, MI: Lewis Publ. 270 pp.

107. Mackenzie, F. T., Agegian, C. R. 1989. Biomineralization and tentative links to plate tectonics. In *Origin, Evolution, and Modern Aspects of Biomineralization in Plants and Animals,* ed. R. E. Crick, pp. 11–27. New York: Plenum

108. Maragos, J. E. 1972. *A study of the ecology of Hawaii reef corals.* PhD thesis. Univ. Hawaii. 290 pp.

109. Marshall, S. M., Orr, A. P. 1931. Sedimentation on Low Isles Reef and its relation to coral growth. *Sci. Rep. Great Barrier Reef Expedition* 1:94–133

110. Mitchell, J. F. B., Manabe, S., Meleshko, V., Tokioka, T. 1990. Equilibrium climate change—and its implication for the future. In *Climate Change: The IPCC Assessment,* ed. J. T. Houghton, G. J. Jenkins, J. J. Ephraums, pp. 131–64. Cambridge: Cambridge Univ. Press

111. Morse, J. W., Mackenzie, F. T. 1990. *Geochemistry of Sedimentary Carbonates.* New York. Elsevier. 707 pp.

112. Muscatine, L., Falkowski, P. G., Dubinsky, Z., Cools, P., McCloskey, L. R. 1989. The effect of external nutrient resources on the population dynamics of zooxanthellae in a reef coral. *Proc. R. Soc. Lond. Ser. B* 236:311–24

113. Muscatine, L., Porter, J. W. 1977. Reef corals: mutualistic symbioses adapted to nutrient-poor environments. *Bioscience* 27:454–59

114. Muthiga, N. A., Szmant, A. 1987. The effects of salinity stress on the rates of aerobic respiration and photosynthesis in the hermatypic coral Siderastrea siderea. *Biol. Bull.* 173:539–51

115. National Research Council. 1991. *Opportunities in the Hydrologic Sciences.* Washington, DC: Natl. Acad. Press. 348 pp.

116. Neumann, A. C., Macintyre, I. 1985. Reef response to sea level rise: Keep up, catch up or give up. *Proc. Fifth Int. Coral Reef Cong., Tahiti.* 3:105–10

117. Ott, B. 1975. Community patterns on a submerged barrier reef at Barbados, West Indies. *Int. Revue Gesamten. Hydrobiol.* 60:719–36

118. Paulay, G. 1988. *Effects of glacio-eustatic sea level fluctuations and local tectonics on the marine fauna of oceanic islands.* PhD thesis. Univ. Wash., Seattle

119. Paulay, G. 1991. Late Cenozoic sea level fluctuations and the diversity and species composition of insular shallow water marine faunas. In *The Unity of Evolutionary Biology: Proc. Fourth Int. Congress of Systematic and Evolutionary Biology,* ed. E. C. Dudley. Portland: Dioscorides

120. Plath, D. C., Johnson, K. S., Pytkowicz, R. M. 1980. The solubility of calcite—probably containing magnesium—in seawater. *Mar. Chem* 10:9–29

121. Porter, J. W., Fitt, W. K., Spero, H. J., Rogers, C. S., White, M. W. 1989. Bleaching in reef corals: Physiological and stable isotopic responses. *Proc. Natl. Acad. Sci. USA* 86 (Ecology): 9342–46

122. Potts, D. C. 1991. Evolution of reef-building corals during periods of rapid global change. In *The Unity of Evolutionary Biology: Proc. Fourth Int. Congr. of Systematic and Evolutionary Biology,* ed. E. C. Dudley. Portland, Dioscorides

123. Ramanathan, V., Collins, W. 1991. Thermodynamic regulation of ocean warming by cirrus clouds deduced from observations of the 1987 El Niño. *Nature* 351:27–32

124. Raup, D. M., Boyajian, G. E. 1988. Patterns of generic extinction in the fossil record. *Paleobiology* 14:109–25

125. Rowan, R., Powers, D. A. 1991. A molecular genetic classification of zooxanthellae and the evolution of animal-algal symbiosis. *Science* 251: 1348–51

126. Roy, K. J., Smith, S. V. 1971. Sedi-

mentation and coral reef development in turbid water: Fanning lagoon. *Pac. Sci.* 25:234–48

127. Ruddiman. W. F. 1985. Climate studies in ocean cores. In *Paleoclimate Analysis and Modeling*, ed. A. D. Hecht, pp. 197–257. New York: Wiley

128. Salm. R. V. 1990. IUCN Coastal Zone Management Project 9571, Sultanate of Oman. *CZMP4:F6*

129. Sandeman, I. M. 1988. Coral bleaching at Discovery Bay, Jamaica: a possible mechanism for temperature-related bleaching. In *Mass Bleaching of Corals in the Caribbean: a Research Strategy. Research report 88-2*, ed. J. Ogden, R. Wicklund. Rockville. Md: NOAA Undersea Res. Prog., pp. 46–48

130. Savina. L. A. 1991. Naturally occurring and laboratory induced bleaching in two Caribbean coral species. *Am. Zool.* 31(5):48A

131. Sheehan. P. M. 1985. Reefs are not so different—they follow the evolutionary pattern of level-bottom communities. *Geology* 13:46–49

132. Shen, G. T., Sanford, C. L. 1990. Trace-element indicators of climate change in annually bonded corals. In *Global Ecological Consequences of the 1982–83 El Niño*, ed. P. W. Glynn, pp. 255–83. New York: Elsevier

133. Siebeck. O. 1988. Experimental investigation of UV tolerance in hermatypic corals (Scleractinia). *Mar. Ecol. Prog. Ser.* 43:95–103

134. Skirrow, G. 1975. The dissolved gases—carbon dioxide. In *Chemical Oceanography* ed. J. P. Riley, G. Skirrow, pp. 1–192. London: Academic

135. Smith, A. D., Roth. A. A. 1979. Effect of carbon dioxide concentration on calcification in the red coralline alga *Bossiella orbigniana. Mar. Biol.* 52:217–25

136. Smith, J. B., Tirpak. D., ed. 1989. *The Potential Effects of Global Climate Change on the United States. Policy, Planning, and Evaluation (PM-221), EPA-230-05-89-050.* Washington. DC: US Environ. Protection Agency. 412 pp.

137. Smith, R. C., Baker, K. S. 1980. Stratospheric ozone, middle ultraviolet radiation and carbon-14 measurements of marine productivity. *Science* 208:592–93

138. Smith, S. V. 1983. Coral reef calcification. In *Perspectives on Coral Reefs*, ed. D. G. Barnes. pp. 240–47. Manuka, Aust: Brian Clouston

139. Smith, S. V. 1985. Physical, chemical and biological characteristics of CO_2

gas flux across the air-water interface. *Plant. Cell Environ.* 8:387–98

140. Smith, S. V., Henderson, R. S. 1978. Phoenix Island report. I: An environmental survey of Canton atoll lagoon 1973. *Atoll Res. Bull.* 221:183

141. Smith, S. V., Jokiel, P. L. 1978. Water composition and biogeochemical gradients in the Canton Atoll lagoon. *Atoll Res. Bull.* 221:15–53

142. Smith, S. V., Kimmerer, W. J., Laws, E. A., Brock, R. E., Walsh, T. W. 1981. Kaneohe Bay sewage diversion experiment: perspectives on ecosystem responses to nutritional perturbation. *Pac. Sci.* 35:279–395

143. Smith, S. V., Pesret, F. 1974. Processes of carbon dioxide flux in the Fanning Island lagoon. *Pac. Sci.* 28:225–45

144. Smith, S. V., Veeh, H. H. 1989. Mass balance of biogeochemically active materials (C, N, P) in a hypersaline gulf. *Estuarine, Coastal Shelf Sci.* 29:195–215

145. Stanley, S. M. 1984. Temperature and biotic crises in the marine realm. *Geology* 12:205–8

146. Stoddart, D. R. 1969. Ecology and morphology of recent coral reefs. *Biol. Rev. Cambridge Philos. Soc.* 44:433–98

147. Strom. R. M., Braman, R. S., Jaap, W. C., Dolan. P., Donnelly, K. B., Martin. D. F. 1991. Analysis of selected trace metals and pesticides offshore of the Florida Keys. *Florida Scientist* 54 In press

148. Swinbanks, D. 1991. Algae to the rescue. *Nature* 350:267

149. Szmant. A. M., Gasser, M. P. 1990. The effects of prolonged "bleaching" on the tissue biomass and reproduction of the reef coral *Montastrea annularis. Coral Reefs* 8:217–24

150. Tans, P. P., Fung, I. Y., Takahashi, T. 1990. Observational constraints on the global atmospheric CO_2 budget. *Science* 247:1431–38

151. Vaughan, T. W. 1916. The results of investigations of the ecology of the Floridian and Bahamian shoal-water corals. *Proc. Natl. Acad. Sci. USA* 2:95–100

152. Veron, J. E. N., Kelley, R. 1988. Species stability in reef corals of Papua New Guinea and the Indo-Pacific. *Memoirs Aust. Paleontolog.* 6:1–69

153. Vicente, V. P. 1990. Response of sponges with autotrophic endosymbionts during the coral-bleaching episode in Puerto Rico. *Coral Reefs* 8:199–202

154. Walker, K. I., Ormond, R. F. G. 1982.

Coral death from sewage and phosphate pollution at Aqaba, Red Sea. *Mar. Pollution Bull.* 13:21–25

155. Ware, J. R., Smith, S. V., Reaka-Kudla, M. L. 1992. Coral reefs: sources or sinks of atmospheric CO2? *Coral Reefs.* In press

156. Warrick, R. A., Oerlemans, H. 1990. Sea level rise. In *Climate Change: The IPCC Assessment.* ed. J. T. Houghton, G. J. Jenkins, J. J. Ephraums, pp. 257–82. Cambridge, Cambridge Univ. Press

157. Warwick, R. M., Clarke, K. R., Suharsono 1990. A statistical analysis of coral community responses to the 1982–83 El Niño in the Thousand Islands, Indonesia. *Coral Reefs* 8:171–79

158. Wells, S. M., ed. 1988. *Coral Reefs of the World.* Vol. 1–3. Cambridge: IUCN

159. Wetzel, R. G., Grace, J. B. 1983. Aquatic plant communities. In *CO2 and Plants: The Response of Plants to Rising Levels of Atmospheric Carbon Dioxide,* ed. E. R. Lemon, pp. 223–280. *AAAS Selected Symposium 84* Boulder, Colo: Westview

160. White, J. K. F. 1980. *Distribution, recruitment, and development of the borer community on shallow Hawaiian reefs.* PhD thesis. Univ. Hawaii 223 pp.

161. Wigley, T. M. L., Barnett, T. P. 1990. Detection of the greenhouse effect in the observations. In *Climate Change: The IPCC Assessment,* ed. J. T. Houghton, G. J. Jenkins, J. J. Ephraums, pp.

239–56. Cambridge: Cambridge Univ. Press

162. Wolanski, E., Pickard, G. L. 1983. Upwelling by internal tides and Kelvin waves at the continental shelf break on the Great Barrier Reef. *Aust. Jour. Mar. Freshwater Res.* 34:65– 80

163. Worrest, R. C. 1982. Review of literature concerning the impact of UV-B radiation upon marine organisms. In *The Role of Solar Ultraviolet Radiation in Marine Ecosystems,* ed. J. Calkins, pp. 429–57. New York: Plenum

164. Worrest, R. C. 1983. Impact of solar ultraviolet-B radiation (290–320 nm) upon marine microalgae. *Physiol. Plant* 58:428–34

165. Worrest, R. C., Grant, L. D. 1989. Effects of ultraviolet-B radiation in terrestrial plants and marine organisms. In *Ozone Depletion: Health and En- vironmental Consequences,* ed. R. R. Jones, T. Wigley, pp. 198–206. New York: Wiley

166. Yamazato, K. 1970. Calcification in a solitary coral *Fungia scutaria* Lam- ark, in response to environmental fac- tors. *Bull. Sci. Engineer Div., U. Ryukyus, Math. Nat. Sci.* 13:59–122

167. Yellowlees, D. 1991. Land use patterns and nutrient loading of the Great Barrier Reef region. *Proc. Workshop, Nov. 17–18, 1990, Townsville. Sir George Fisher Cent. Trop. Mar. Stud. Queensland, Aust.*

168. Yonge, C. M. 1931. The biology of reef building corals. *Sci. Rep. Br. Mus. (Nat. Hist.)* 1:353–91.